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MANTLE CAVITY, HABITS, AND HABITAT
IN THE BLIND LIMPET,
LEPETA CONCENTRICA MIDDENDORFF¹

BY

C. M. YONGE
University of Glasgow

INTRODUCTION

The tribe Patellacea (Docoglossa) comprises three families, the Acmaciidae, Patellidae, and Lepetidae, better considered in this order than with the more specialized Patellidae first as in Thiele (1931). In the first of these there is a single aspidobranch etenidium turned on its side and directed to the right with the addition, in the genus *Lottia*, of secondary pallial gills. In the Patellidae these gills alone occur, there being no etenidium. The ring of gills is interrupted anteriorly in *Patina* (*Helcion*), *Nacella*, and *Cellana* but is complete in *Patella*. Details of the structure and of the ciliary currents in both etenidia and pallial gills are given elsewhere (Yonge, 1947) where the various means of detecting the presence of suspended matter by osphradia and sensory streaks are described, and also the manner in which this is accumulated and finally removed. In *Acmaca* (*Patelloida*) *tessulata* and *A. virginea* both exhalant current and collected sediment pass back along the pallial grooves which they leave in the mid-line posteriorly.² But the pres-

1. From the Friday Harbor Laboratory, University of Washington.

2. This is not true of many Pacific species of *Acmaca* where the greater water movements apparently ensure cleansing of the pallial grooves (personal observations at Pacific Grove).

ence of the secondary gills in the pallial grooves makes this impossible in other genera. In *Lottia gigantea*, which lives intertidally on exposed and usually steeply sloping or precipitous rocks, cleansing is largely the work of water movements (Abbott, 1956). In *Patina* the bulk of the waste material is embedded in mucus secreted by a glandular streak around the margin of the foot. In this state it is carried to the front of the foot by ciliary action. Material which collects on the mantle margins is carried to the right side of the head and there removed in the relatively weak exhalant current. In *Patella*, where a glandular streak occurs along the side of the foot in young individuals only, sediment is conveyed by cilia to the middle of the right side where it accumulates on the side of the foot for periodic expulsion, in a manner reminiscent of the expulsion of pseudofaeces in bivalves, by sudden contraction of the shell muscles (Yonge, 1947).

It will be noted that in these limpets—all of them intertidal in habitat—creation of a respiratory current by either etenidium or pallial gills produces the need for mechanisms to rid the mantle cavity of matter carried in suspension in this current. In the Lepetidae, however, neither etenidium nor secondary gill is present while these limpets are sublittoral in habitat. It follows that the nature of the ciliary currents, never previously observed, within the nuchal cavity and pallial grooves becomes a matter of some interest.

FAMILY LEPETIDAE

Apart from the absence of any form of respiratory outgrowth, members of this family are characterized by lack of eyes, by a radula which possesses a median tooth absent in the Acaecidae, and by the lateral prolongation of the head into a pair of labial processes (fig. 2). The few species of the two constituent genera, *Lepeta* Gray 1847 and *Propilidium* Forbes & Hanley 1849, are sublittoral inhabitants of cold and polar seas, especially in the Northern Hemisphere. Although *Lepeta cacca* Müller, the northern blind limpet, which occurs on both sides of the North Atlantic, is probably the best known species, repeated attempts to obtain this by dredging in the Clyde Sea area (where it has been recorded) proved fruitless. It was therefore particularly gratifying, while working at the Friday Harbor Laboratory of the University of Washington during the summer of 1959, to find that the closely related *L. (Cryptotenidia) concentrica* Middendorff was common in the waters around the San Juan Islands. It is a pleasure, at this point, to record gratitude to Dr. R. L. Fernald, Acting Director of the Laboratory, to Dr. Dixy Lee Ray, and to other colleagues and fellow workers.

LEPETA CONCENTRICA MIDDENDORFF

SHELL. Summarizing the description by Oldroyd (1927), the shell is depressed and conical with the apex directed forward and the anterior slope about one-third or less the length of the shell. The surface of this is usually light brown and bears faint radiate striations. The outline is oval but a little narrower in front; the anterior slope is slightly concave and the posterior slope convex. The edges of the shell are smooth and the inside is polished with the anterior terminations of the muscle scar very slightly behind the apex and with the posterior region much nearer to the margin of the shell. A length of about 20 mm., a breadth of 16 mm., and a height of 8 mm. are attained.

DISTRIBUTION. Oldroyd reports the presence of this species from Icy Cape in the Arctic to Puget Sound and also in the Okhotsk Sea. Around the San Juan Islands it is common on suitable bottoms, certainly down to 25 fathoms as reported by Oldroyd and probably deeper. Like all members of this family, it is exclusively sublittoral. It never occurs in numbers together and

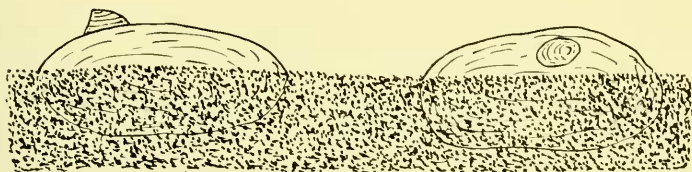


Figure 1. *Lepeta concentrica*, habitat on stones lying on mud at about 45 meters depth in Griffin Bay, San Juan Island, showing isolation of individual limpets. $\times \frac{1}{2}$.

was most characteristically taken in dredgings in some 45 meters in Griffin Bay off the southeast of San Juan Island. Here the bottom is of dense mud on the surface of which smooth, rounded stones about 7 cm. in greatest diameter apparently occur in some numbers. The upper surface of these bears a variety of encrusting organisms, notably bryozoans, balanoids, and serpulids, and with them there was usually found one and very occasionally two of these limpets (see fig. 1). In these depths there is no algal growth so that the limpets must feed largely, if not exclusively, on the organic detritus which will settle continuously out of the water in such regions of mud deposition. Steady deposition of food is clearly essential owing to the small area of feeding surface—not more than about 30 sq. cm. in most cases—available to any one limpet, because the surrounding mud represents an impassable barrier to such animals. Clearly on more extensive rocky surfaces they will not be so confined, but there will also be less deposition on these so that a wider feeding range will be necessary.

EXTERNAL STRUCTURE. Examination of the animal from the ventral aspect (fig. 2) reveals the great simplicity of external structure. The mantle is fringed with a single row of minute and evenly distributed tentacles, not comparable with the pallial tentacles in *Patella* and notably smaller than those in *Acmaca* (Yonge, 1947). The head bears a pair of short, rather stout tentacles without eyes. Laterally it is extended into the distinctive pair of labial processes which will sweep the surface of the rock on either side of the mouth as the animal moves and feeds. They may have sensory powers or could perhaps push food toward the mouth, but if so by muscular and not ciliary action because the head is not ciliated. The slitlike mouth opens repeatedly to expose the radula.

The nuchal cavity is shallow and contains only the openings of the anus and of the kidneys, situated together on papillae on the right side. Ctenidium, osphradia, and also, as noted by Thiem (1917), the sensory streaks present in other Patellacea are absent. In justification of an earlier surmise (Yonge, 1947), the loss of these sensory structures has been found to be accompanied by loss of ciliation throughout the nuchal cavity.

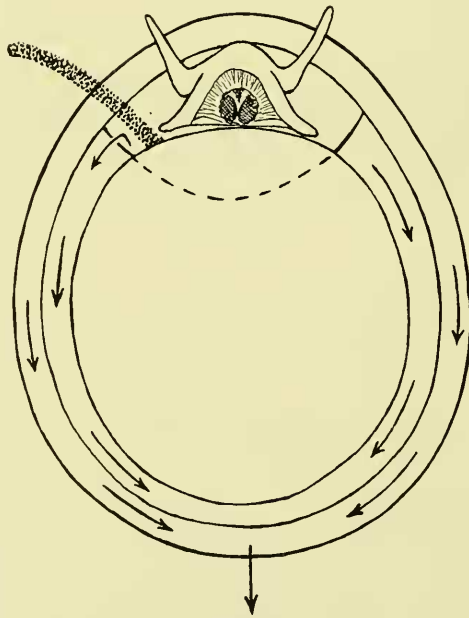


Figure 2. *Lepeta concentrica*, ventral aspect showing head with labial processes and tentacles (no eyes), foot, pallial grooves and extent, indicated by broken line, of nuchal cavity containing anus and renal openings. Arrows indicate direction of ciliary currents in pallial grooves; faecal rod emerging from nuchal cavity on right side. $\times 4$.

In the absence of secondary gills, the pallial grooves are featureless. The usual blood vessel runs around the mantle, a little distance from the margin. Ciliation both on the mantle (except around the head) and on the sides of the foot is well developed and, as indicated by the arrows in figure 1, material is carried rapidly to the midline posteriorly where the groove is shallowest and there, consolidated in mucus, it is passed out.

While disposal of sediment from the pallial grooves thus follows the same course as in *Acmaea tessulata* and *A. virginica* (Yonge, 1947), this is not true for the faeces. The small faecal pellets characteristic of these species of *Acmaea* (Moore, 1931) are conveyed along the right pallial groove for similar posterior expulsion. In *L. concentrica*, however, the faeces in the form of long, slightly curved rods are pushed directly out from the right side of the head, as shown in figure 2. These rods have a diameter of 0.5 mm. and are often over 1 cm. long; they are mud colored and appear to be almost entirely composed of minute particles of sand. They are produced in very great quantity.

BEHAVIOR. Specimens of *L. concentrica* were observed in the aquarium and also in bowls of sea water under the binocular dissecting microscope. They differ in behavior from intertidal Acmaeidae and Patellidae in two important respects. When exposed to air on the surface of a stone they invariably move down below water level, and they also move about more continuously and more rapidly. There is every indication that they are engaged primarily in collecting detritus rather than in scraping the rock surface. When moving, the shell margins are just clear of the rock surface by perhaps as much as 0.5 mm. The minute pallial tentacles may be just visible in some areas, but the cephalic tentacles are not usually to be seen except when the animal is viewed as it moves over the curved edge of a stone. The long faecal rods are continuously being extruded on the right side of the head, indicating corresponding activity in feeding. The only discernible current, and that only gentle, emerges from under the shell posteriorly.

DISCUSSION

While retaining the form and general habit of the other Patellacea, the Lepetidae have exploited the possibilities of life in the sublittoral (in some cases to considerable depths). This has followed the loss of the etenidium but, unlike the Patellacea, without the appearance of secondary gills. The apparent loss in respiratory efficiency may well have been made good by the possibilities of uninterrupted respiration under conditions of continuous submergence. In any case the loss of respiratory currents, whether caused locally by a etenidium or more generally by pallial gills, has the major and probably all important compensating advantage of removing the problem represented

by the need for disposing of sediment entering with such currents. Now that sediment is no longer carried into the nuchal cavity or the pallial grooves, the osphradia and the sensory streaks needed for its detection (Yonge, 1947) disappear. The nuchal cavity is devoid of cilia while ciliation in the pallial grooves is adequate to clear these of any sediment raised as the animal moves.

With the sublittoral habit and the habit of feeding on organic deposits (doubtless including bottom diatoms, etc.) may be correlated the loss of sensory equipment represented by the disappearance of the eyes and reduction of both cephalic and pallial tentacles. The characteristic labial processes may possibly aid in collection of food which, in the form of constantly settling deposits, needs to be widely scooped up by the continuously moving animal.

The Lepetidae may thus be regarded as a group of archaeogastropod which, like the Patellidae, are to be derived, as originally suggested on purely morphological grounds by Thiem (1917), from the more primitive, because still etenidial-bearing, Aemaeidae. But whereas both groups have lost the etenidium, in the Patellidae this has been replaced by secondary gills which, with the elaboration of better methods for ridding the mantle cavity of sediment, increase efficiency in the intertidal habitat, while in the Lepetidae it is loss of this structure accompanied by change in habits which has made sublittoral life possible, under conditions, moreover, where there is much deposition of sediment (see fig. 1).

The course of evolution within the Aemaeidae and Patellidae, involving change in conditions in the mantle cavities of *Acmaea* (*Patelloida*), *Lottia*, *Patina*, and *Patella*, has been outlined and illustrated elsewhere (Yonge, 1947, fig. 23). The present study would derive the Lepetidae also from the Aemaeidae. Palaeontological evidence supports these conclusions. According to Wenz (1938), the Aemaeidae appeared in the middle of the Triassic to be followed by the Patellidae near the end of the Jurassic and by the Lepetidae at the beginning of the Miocene.

The sublittoral habit in limpets is not common. The great majority of archaeogastropod limpets, i.e., the Fissurellidae and the Patellacea, are intertidal. So also are the marine pulmonate limpets such as *Siphonaria* (Yonge, 1952, 1960) and *Trimusculus* (Yonge, 1958, 1960), and also *Hippomix* (Yonge, 1953, 1960) among mesogastropods. Apart from some mesogastropod ciliary-feeding Calyptraeidae and Capulidae, the only gastropod limpets (i.e., excluding the monoplacophoran *Neopilina*) occurring in deep water appear to be members of the Coeculinacea, such as *Addisonia*, in which the etenidium extends back along the right pallial groove (Dall, 1889). Although possessing an aspidobranch etenidium, in all other respects these animals are mesogastropods with the means of internal fertilization and direct development. They live in great depths and for that reason have never, unfor-

tunately, been examined in life. Strictly speaking, therefore, the Lepetidae appear as the only exclusively sublittoral group of truly archaeogastropod limpets.

SUMMARY

The family Lepetidae, as exemplified by *L. concentrica* here examined, is composed of forms which are characteristically adapted for life in the sublittoral where they invariably occur.

Lepeta concentrica feeds on detritus which involves continual movement over the feeding surface which may not exceed 30 sq. cm. This indiscriminate feeding may explain the loss of eyes and reduction of pallial and cephalic tentacles. The characteristic labial processes may be concerned with drawing food toward the mouth.

Neither ctenidium nor pallial gills occur. Correlated with the absence of indrawn sediment, osphradia and sensory streaks present in other Patellacea are lacking. The shallow nuchal cavity is unciliated; in the pallial grooves particles are carried posteriorly.

The position of the Lepetidae within the Patellacea (Docoglossa) is considered. Loss of the ctenidium present in the more primitive Acmacidae, together with change in habits, accounts for their movement into the sublittoral which they are the one group of the Archaeogastropoda successfully to exploit.

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